THE LOGGERHEAD TURTLE, *CARETTA CARETTA* IN QUEENSLAND: FEEDING ECOLOGY IN WARM TEMPERATE WATERS

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Gut contents and faecal samples from 53 loggerhead turtles, *Caretta caretta*, from the Bundaberg coast, Hervey Bay, Sandy Straits, Moreton Bay and Gold Coast regions of southern Queensland continental shelf waters were examined. *C. caretta* in these coastal waters are carnivorous, consuming at least 94 taxa of benthic and near benthic organisms. Large immature and adult *C. caretta* are specialised for feeding on slow moving, hard bodied invertebrate prey with molluscs and crustaceans being the most commonly consumed taxa. Four feeding methods were identified for these *C. caretta*. The specific prey species selected was a function of the turtle's feeding area rather than its sex or size. As individuals their diet is unpredictable with some variability in the diet being attributed to individual preference. ❐ *Loggerhead turtle, Caretta, feeding ecology, southeast Queensland.*

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The loggerhead turtle, *Caretta caretta,* is carnivorous and feeds on a very wide range of prey species. While it preys primarily on benthic invertebrates such as crustaceans, bivalves and gastropods, it consumes many other taxa including jellyfish, sea pens, sea urchins, holothurians, tunicates, and fish (Bleakney, 1967; Burke & Standora, 1993; Ernst & Barbour, 1989; Gudynas, 1980; Plotkin, 1996; Porter, 1972; Preen, 1996). Some of this diversity in diet is a function of the life history phase of the turtles. *C. caretta*, typical of cheloniid turtles, occupies a wide range of habitats throughout its life history (Carr, 1986; Dodd, 1988; Limpus, 1985, 1994). Eggs are laid in sandy tropical and warm temperate beaches. The hatchlings leave the beaches and disperse within days into deep water from where they enter a pelagic phase, being dispersed by ocean currents. For the first years of their life they occupy open ocean surface waters before recruiting to live in widely dispersed feeding areas over the continental shelf. Breeding adults migrate from their feeding areas to their traditional breeding sites and occupy courtship and internesting habitats within the waters adjacent to the nesting beaches for some months during each breeding season. At the completion of the breeding season they return to their respective feeding areas. Feeding by *C. caretta* is largely restricted to the pelagic phase where the young turtles utilise planktonic prey at or near the ocean surface (Plotkin, 1996; van Nierop & den Hartog, 1984) and inshore shallow waters where the larger sized turtles feed predominantly on benthic prey (Conway, 1994; Plotkin et al., 1993; Moodie, 1979). The breeding adult does not feed while ashore for egg laying. Similarly, while in the courtship and internesting habitats, the breeding female does not feed or substantially reduces her feeding, while she is in this egg production phase (CJL unpubl. data). The hatchlings do not feed while in the nest, while crossing the beach or in the inshore waters as they disperse from the nesting beach.

The eastern Australian *C. caretta* stock (Bowen et al., 1994) is endangered with a declining breeding population (Limpus & Reimer, 1994). As part of general studies to understand their biology, we describe the diet of adult and large immature *C. caretta* feeding in inshore warm temperate waters of southeastern Queensland.

METHODS

Gut contents were obtained opportunistically from *C. caretta* from southeastern Queensland during 1989-1998. The study area extended from the Kolan River near Bundaberg (24°35'S, 152°07'E) to the Gold Coast (28°02'S, 153°26'E). Habitats utilised by *C. caretta* encompass rocky reefs, bays, estuaries and coastal open waters.

Free ranging *C. caretta* were captured during mark-recapture studies (Limpus, 1978, 1985; Limpus et al., 1994). Dead and moribund *C. caretta* were obtained through the Queensland Parks and Wildlife Service (QPWS) marine wildlife stranding program. Faecal samples were obtained from the live turtles. Digestive tract contents were obtained during necropsy of the turtles from the stranding program. The amount of gut contents collected was dependent on the state of decomposition of the carcass but, where possible, the entire alimentary tract was sampled. For each sample, the turtle's sex, age class, breeding status, midline curved carapace length (CCL), injuries, cause of death, date, and location were recorded. Carcasses were selected only if the body organs were intact. While the turtles were not feeding at the point of stranding, given the limit on state of decomposition, it is presumed that they would have fed in the adjacent waters. For ease of description, gut contents are identified by the tag number of the turtles or the museum specimen numbers. All except one sample were from non breeding turtles in or adjacent to their presumed feeding areas.

No sub-sampling was taken of large samples. Samples with fleshy biomass were fixed in 5-10% formalin solution. Samples of predominantly hard skeletal remains, including mollusc and crustacean exoskeletons, were dried and stored. Prior to sorting, samples which had been stored in formalin were rinsed in freshwater and spread on sorting trays to remove most of the moisture. Prey items from the Brachiopoda, Mollusca, Crustacea and Osteichthyes were identified to species or genus level where possible. Prey items from the Porifera, Cnidaria and Echinodermata were identified at higher taxonomic levels. No attempt was made to identify the algae and seagrass. As each prey taxon was identified, the number of individuals present was counted using identifying features of fragments that remained intact through the feeding and digestive process. Decapod crustaceans were counted by the number, size, and orientation (left/right) of chelae, and to a lesser extent, mandibles. The number of hinges and the orientation of valves assisted with bivalve counts. With gastropods, intact spires were the primary indicator of the number of individuals consumed, but at times, counts of opercula (e.g. *Turbo* spp., *Strombus* spp.) were more appropriate. Sand, stone, coral fragments, dead shell (identified by eroded and dull inner shell surfaces), charcoal and tree bark were treated as incidentally ingested debris. Queensland Museum staff and private shell collectors assisted with the identification of prey items. For analysis, the samples were grouped by geographic origin: Bundaberg coast, Hervey Bay, Sandy Straits, Moreton Bay and Gold Coast. For the purposes of this analysis, a dominant prey species was defined as one comprising >5% of a sample by either the number of individual prey items present or by volume. Volume was used in the analysis of six samples where there were very large differences in the sizes of prey species (see Tables 2,4).

RESULTS

Fifty-three samples included 6 faecal samples and 47 digestive tract contents. The geographic origins of samples were the Bundaberg Coast (n=16), Hervey Bay (Woodgate - Burrum Heads (3); Sandy Cape (2), Sandy Straits (2), Moreton Bay (22), and Gold Coast - Jumpinpin (8). Prey from at least 94 taxa representing 8 Phyla were identified (Table 1): 36 species of crustaceans, 43 molluscs (18 gastropod, 23 bivalve, 1 scaphopod, 1 cephalopod), 1 poriferan, 2 cnidarians, 1 brachiopod, 3 echinoderms, 1 urochordate, and at least 7 Osteichthyes.

Most food items were crushed and the soft tissues and some or all of the skeletal fragments ingested. A small range of items were ingested whole, including some fish, bêche-de-mer and small molluscs. The largest intact prey was a porcupine fish (Family Diodontidae, 21cm), lodged in the oesophagus, and which probably caused the death of the turtle (tag=Z1819). The smallest intact prey were the gastropod *Olivia caldania* (1.4cm) and the scaphopod *Dentalium sp.* (2.4cm), both in the same turtle, T89145. It is presumed that these shells had been ingested incidentally and not crushed when the turtles had targeted larger prey. Other taxa that were considered to be ingested accidentally were seagrass and barnacles: there were only isolated blades of seagrass in the gut contents from 4 *C. caretta*; some barnacles were attached to other targeted prey species such as portunid crabs. The greatest abundance of prey from an entire gut content was 670 individuals and the largest number of a single species was 565 *Solen vagenoides* (Chinese fingernail shell). Where there were >400 prey items occurred in a sample, they primarily consisted of a single species: 36% of samples comprised =90% of a single species and 15% of samples were made up of a single species.

TABLE 1. *Caretta caretta* prey species by regions within subtropical Queensland. The value in each cell denotes the number of turtles recorded with each prey species. The percentage range that each prey species contributed to a turtle's diet sample is shown in parenthesis. * indicates material which was considered incidental and not included in the analysis of prey species; # identified fish included: porcupine fish (*Diodon*), flathead (*Platycephalus*), bigeye (*Priacanthus*), flounder (*Pseudorhombus*), whiting (*Sillago*) and wrasse (Labridae).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
No. turtles in sample		n=16	n=5	n=2	n=22	n=8
Phylum ARTHROPODA						
Class Cirripedia	* barnacle, unidentified	2(1.1-1.3%)	2(0.3-4.3%)	1(1.4%)	7(0.2-1.4%)	1(<1%)
Class Malacostraca						
Order Decapoda						
Infra-order Anomura						
Family Diogenidae	*Clibanarius* sp.	9(2.7-31.8%)				
	Clibanarius taeniatus				1(0.4%)	
	Dardanus imbricatus	12(5-90.6%)	1(16.7%)		1(16.7%)	
Infra-order Brachyura						
Family Calappidae	*Calappa (?) hepatica*	1(2.2%)				
	Calappa sp.	2(2.7-4.5%)				
	Matuta sp.		1(8.3%)			1(20%)
Family Goneplacidae	*Eucrate dorsalis*	1(0.2%)			12(0.6-100%)	
	Galene bispinosa				8(0.6-55%)	
	Galene cf *bispinosa*				1(1.6%)	
Family Leucosiidae	*Leucosia* sp.	8(0.2-7.1%)	2(7.7-8.3%)		2(12.5-16.7%)	
	Myra affinis	4(0.6-6.9%)	1(10%)		1(0.6%)	
	Myra sp.	1(1.7%)				
Family Parthenopidae	*Cryptopodia queenslandi*	5(0.1-4.5%)				
	Parthenope nodosa	8(0.2-31.8%)				
	Parthenope (?) valida	1(0.2%)				
Family Pinnotheridae	*Xenophthalmus pinnotheroides*		1(1.3%)			
Family Portunidae	*Charybdis natator*	3(0.5-6.9%)	1(25%)			3(2.5-20%)
	Portunus pelagicus	1(2.89%)	1(1.3%)		4(3.5-100%)	2(2.5-5%)
	Portunus sanguinolentus	4(1.4-25%)	2(25-90%)		11(0.2-50%)	3(2.5-20%)
	Thalamita sima				3(0.2-48.4%)	
	portunid crab, unidentified 1	1(3.8%)			3(2.38-50%)	1(5%)
	portunid crab, unidentified 2	1(0.5%)				
	portunid crab, unidentified 3	1(1.72%)				
	portunid crab, unidentified 4				1(17.5%)	
	portunid crab, unidentified 5	1(0.5%)				
Family Raninidae	*Ranina ranina*					4(1.7-40%)
Family Xanthidae	*Halimede ochtodes*	2(0.5-5.2%)				
-	crab, unidentified 6	1(0.5%)				
	crab, unidentified 7	1(1.72%)				
	crab, unidentified 8	1(1.4%)				
	crab, unidentified 9				1(5%)	
	unidentified (fragment)	1(33%)			2(1-50%)	
Infra-order Penaeidae	penaeid prawn					1(<5%)
Order Stomatopoda	*Squilla* sp.				3(3.1-10%)	
Phylum BRACHIOPODA						
Family Lingulidae	*Lingula murphiana*		1(90%)			

TABLE 1 (*cont.*).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
Phylum CHORDATA						
Class Ascidiacea	ascidian, unidentified				2(14.2-22.2%)	
Class Osteichthyes	fish, multiple species #	1(100%)	1(25%)		3(2.4-50%)	8(20-95%)
Phylum CNIDARIA						
Class Anthozoa						
Order Gorgonacea	sea whip, unidentified				1(20%)	
Order Actiniaria	anemone, unidentified	1(0.6%)				
Phylum ECHINODERMATA						
Class Echinoidea	sea urchin, unidentified	1(100%)			2(0.6-2.2%)	
Class Holothuroidea	bêche-de-mer, unidentified				1(5%)	
Class Stelleroidea	starfish, unidentified	1(90%)				
Phylum MOLLUSCA						
Class Bivalvia						
Order Arcoida						
Family Arcidae	*Anadara trapezium*	3(0.2-18.4)	1(6.3)	1(100)	2(60.7-100)	
Family Glycymeridae	*Glycymeris holsericus*	1(2.6)				
Order Mytiloida						
Family Anomiidae	*Patro australis*		1(25)			
Family Mytilidae	*Botula* sp. (elong. shiny mussel)	1(4.5)				
	Modiolus ostentus	1(100)				
	Stavelia horrida	1(2.6)				
	Trichomya hirsuta				2(18.8-100)	
Family Ostreidae	*Crassostrea commercialis*				1(10.7)	
	Ostrea bresia	1(0.2)				
	Saccostrea commercialis			1(0.7)		
Family Pectinidae	*Annachlamus flabellata*	3(1.3-33)			1(4.5)	
	Amusium balloti	4(0.5-30.4)				
Family Pinnidae	*Atrina pectinata*	6(0.2-63)	1(87)		2(3.6-33.3)	
Family Pteriidae	*Pinctada albina sugillata*	1(2.6)				
	Pinctada fucata		2(1.3-8.3)			
Family Spondylidae	*Spondylus wrightianus*	1(1.4)				
-	oyster fragment				1(5)	
Order Veneroida						
Family Carditidae	*Cardita incrassata*				1(10.7)	
Family Mactridae	*Mactra abbreviata*	1(2.6)				
Family Solenidae	*Solen vaginoides*				1(99.5)	
Family Tridacnidae	*Tridacna maxima*					
Family Veneridae	*Antigona lamellaris*	2(1.4-2.6)	1(2.6)		3(3.6-75)	
Family Crassatellidae	*Eucrassatella cumingii*	1(2.6)	1(2.6)		1(16.7)	
-	unidentified (fragment)	1(0.6)			2(0.2-0.6)	
Class Cephalopoda	octopus, unidentified					2(1.7-2.5)
Class Gastropoda						
Order Archaeogastropoda						
Family Trochidae	*Calthalotia indistincta*			1(0.7)		
	Monilea callifera				1(90)	
Family Turbinidae	*Turbo haynesi*	1(3.1)				

TABLE 1 (*cont.*).

Taxa	Genus/Species/Common name	Bundaberg	Hervey Bay	Sandy Straits	Moreton Bay	Gold Coast
Order Mesogastropoda						
Family Cerithidae	*Pyrazus ebeninus*				1(5)	
Family Naticidae	*Polinices conicus*				1(0.2)	
	Polinices didyma	1(0.6)				
Family Potamididae	*Velacumantus australis*			1(98.6)		
Family Strombidae	*Strombus campbelli*	6(3.3-85.6)			1(91.1)	
Family Tonnidae	*Tonna tessellata*					1(20)
Order Neogastropoda						
Family Buccinidae	*Dolicholatirus thesaurus*	2(0.5-1.8)				
Family Fasciolarinae	*Fusinus colus*	1(0.6)				
Family Muricidae	*Lataxiena fimbriata*	1(1.2)				
Family Olividae	*Oliva caldania*	1(0.2)				
Family Volutidae	*Amoria maculata*	1(0.2)				
	Cymbiolacca complexa	1(0.2)				
	Melo amphora	1(95)				
	Melo sp.					1(<5)
	unidentified fragment	1(0.1)				1(5)
Class Scaphopoda						
Family Dentaliidae	*Dentalium* sp.	1(0.1)				
Phylum PORIFERA	sponge, unidentified	1(2.6)			3(7-50)	
Other	* algae	2(<1)			1(0.3)	
	* seagrass	2(<1)			4(<1)	

A faecal sample comprising both valves of the hairy mussel, *Modiolus ostentatus*, was obtained from a nesting ♀ *C. caretta* during oviposition at Mon Repos near Bundaberg (X37114). This was the only identifiable item obtained as faecal material from the many thousands of nesting females observed. This prey species was not found in any other turtle sample. Given that Bundaberg is outside the geographical distribution of this tropical bivalve species (Lamprell, 1998) and that breeding female marine turtles do not feed, or substantially reduce their food uptake, while away from their home feeding areas during their breeding migrations (C. Limpus, unpubl. data), it is highly unlikely that this food item originated from the Bundaberg coast. Hence this sample was excluded from the following analysis.

Bundaberg coast.

Fifty two species were identified in 14 *C. caretta* samples from the Bundaberg region (Table 1). The mean number of prey species per sample was 8.4 (SD=4.7, range=2-16). Of the 52 prey species only 14 (26.9%) were dominant prey items (Table 2). These *C. caretta* fed mostly on hermit crabs (12/14 individuals), gastropods (5/14 individuals), bivalves (3/14 individuals) and small brachyuran crabs (5/14 individuals). For nine of these turtles the sample comprised many specimens of multiple species of prey. In contrast, for three individuals, a single large item (gastropod [*Melo amphora*], sea urchin and starfish, respectively) dominated the sample. One turtle had many specimens of the hermit crab, *D. imbricatus*, comprising >90% of the gut content. The dominant prey items from the Bundaberg Coast (Table 2) were benthic species that live on or superficially burrow into the substrate. These dominant prey species were slow moving with the exception of the more agile saucer scallop, *A. balloti*.

Hervey Bay.

Sixteen species were identified in the gut contents of five *C. caretta* from the Hervey Bay region (Table 1). The mean number of prey species per sample was 3.8 (SD=1.0, range=2-5). Of the 16 prey species, 12 (75%) were dominant prey items (Table 3). These *C. caretta* fed mostly on bivalves (4/5 individuals), crabs (4/5 individuals) or hermit crab (1/5 individuals) With one exception, this geographic group consumed

TABLE 2. Relative abundance by number of individuals of prey items identified in the gut contents of beach washed *Caretta caretta* (n=14) from the Bundaberg Coast. All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. y' denotes that the species was present in the gut sample at less than the 5% level. Other species present at less than 5% of a gut content within all samples are not listed. * Where there was a very large difference in the size of prey items the abundance has been adjusted to reflect the relative volume of the prey species.

Tag number	N39890	N39891	N39925	N39944	N39961	N39970*	N39975
Date	14.02.94	18.02.94	07.02.94	04.02.94	15.01.94	25.01.93	12.01.93
Sex	♀	♀	♀	♀	♀	♀	♀
Maturity	Adult	Immature	Adult	Immature	Immature	Immature	Adult
Carapace length (cm)	94.7	83.5	93.5	75.5	82.0	83.0	104.5
Latitude	24°52'S	24°50'S	24°49'S	24°52'S	24°47'S	24°58'S	24°49'S
Longitude	152°29'E	152°28'E	152°27'E	152°28'E	152°26'E	152°29'E	152°28'E
Prey Items							
Mollusc, gastropod							
Strombus campbelli		86%		y			10%
Melo amphora							
Mollusc, bivalve							
Ambusium balloti	30%			y			51%
Anadara trapezium		y					
Atrina pectinata	y				y		
Crustacea, hermit crab							
Dardanus imbricatus	22%	5%	18%	70%	50%	5%	17%
Clibanarius sp.	29%	8%	32%	y	5%	5%	10%
Crustacea, brachyuran crab							
Charybdis natator				y	7%		
Halimede ochtodes				y	5%		
Leucosia sp.	y	y		y	5%		7%
Myra affinis	y			y	7%		
Parthenope nodosa	y	y	32%	7%	12%		y
Echinoderm, starfish						90%	
Echinoderm, sea urchin							

Tag number	N39979*	N39985	N39993	T85156	T89145	T89184	Z2029
Date	06.01.93	15.12.92	28.11.92	15.01.95	06.01.96	01.06.96	26.11.96
Sex	♀	♀	♂	♂	♂	♂	♂
Maturity	Immature	Immature	Immature	Immature	Immature	Immature	Immature
Carapace length (cm)	83.0	78.0	85.5	82.7	91.5	91.5	95.1
Latitude	24°48'S	24°48'S	24°47'S	24°58'S	24°40'S	24°40'S	24°43'S
Longitude	152°26'E	152°27'E	152°26'E	152°29'E	152°13'E	152°13'E	152°17'E
Prey Items							
Mollusc, gastropod							
Strombus campbelli		41%		30%	81%		
Melo amphora	95%						
Mollusc, bivalve							
Ambusium balloti		y					
Anadara trapezium				y		18%	
Atrina pectinata			y		y	63%	
Crustacea, hermit crab							
Dardanus imbricatus	5%	43%	91%	27%	11%		
Clibanarius sp.		9%		31%			
Crustacea, brachyuran crab							
Charybdis natator			y				
Halimede ochtodes							
Leucosia sp.			y	y	5%		
Myra affinis				y			
Parthenope nodosa				y	y		
Echinoderm, starfish							
Echinoderm, sea urchin							100%

few prey species, usually with only one species dominating the sample. For example, a single prey species constituted ~90% of the gut content (*A. pectinata*, *P. sanguinolentus*, or *Lingula murphiana*). The prey for this region represented a range of habitats: within the water column (fish), on or superficially burrowed within the substrate surface (*A. pectinata* and crabs) or burrowed deep within the substrate (*L. murphiana*). That 72 *L. murphiana* were the only species present in 1 sample indicates that the turtle was intentionally feeding on this eryptic species to the exclusion of other species.

Sandy Straits.

Four species were identified in the 2 gut contents from the Sandy Straits region (Table 1). The number of prey species per sample ranged 1-3. Two species (50%) were dominant prey items (Table 3). The 2 *C. caretta* had fed almost exclusively on either the gastropod *Velacumantus australis*, or the bivalve *A. trapezium*. Both prey species are epibenthic or superficially burrow.

Moreton Bay.

Thirty-four prey speeies were identified in 22 *C. caretta* samples from the Moreton Bay region (Table 1). The mean number of prey speeies per sample was 3.8 (SD=2.2, range=1-7). Of the 34 prey species, 27 (79%) were dominant prey items making up >5% of any one gut content (Table 4). The *C. caretta* in Moreton Bay had been feeding mostly on crabs (14/21 individuals), especially portunid crabs. When molluses occurred in the sample, they were the major eomponent of the prey (8/21 individuals) and a single species of gastropod or bivalve dominated. Other benthic animals (sea cucumber, sea urchin, sea whip, ascidian and sponge) were taken commonly and many *C. caretta* consumed a wide range of prey species. However, 8 of the 21 turtles ingested a very limited range. Six had gut eontents approaching 100% of a single species of bivalve or erab; two had gut contents with a single gastopod speeies aceounting for ~90%. The majority of the prey items were benthic species that live on or superficially burrow within the substrate, except for the bivalve *S. vagenoides* whieh burrows well below the surface. Most of these prey species are slow moving, although the fish and stomatopod are active species.

Gold Coast - Jumpinpin.

Ten species groups were identified in the gut contents of eight *C. caretta* from the Gold Coast - Jumpinpin region (Table 1). Of these, six (75%) were dominant prey items (Table 5). The *C. caretta* sampled fed predominantly on small fish (8/8 individuals) with six of eight turtles consuming a diet consisting of >90% fish. While some species of fish could be recognised (Table 5) most material could not be identified and is grouped as all fish. Crabs contributed significant amounts to the overall volume of prey ingested by 2/8 individuals. A single speeimen of the gastropod *Tonna tessellata* was a major component of the diet of one turtle. The principal prey items in this area were highly mobile speeies that live close to the substrate and in the adjacent water column (fish). A small amount of the slow moving benthic species that live on the substrate surfaee or superficially burrow were eaten also. There was circumstantial evidence (unpublished data, QPWS stranding database) that at least several of these turtles had been killed during fish trawling activities off this coastline. The prey items identified from these turtles are common among the 'trash fish' discarded from this trawl fishery. There is a high probability that these turtles were scavenging the water column or the substrate for discarded dead bycatch.

COMPARISON AMONG REGIONS. Molluses and crustaceans dominated the diet of *C. caretta* in most areas but not inthe Gold Coast region. However, the dominant species in the diet varied spatially. For example, on the Bundaberg coast the diet included a range of hermit crabs, a gastropod (*S. campbelli*) and a bivalve (*A. balloti*) for the major part of the diet (Table 2). The diet in Moreton Bay was dominated by a range of brachyuran crabs (not hermit crabs) and bivalves (not *A. balloti*) (Table 4). Within a localised area, many turtles displayed idiosyncratic feeding patterns, choosing to feed on individually unique suites of prey.

Over half (54.7%) of *C caretta* in this study had consumed < 5 species of prey. The turtles from the Bundaberg region contained more prey species per sample (8.4 prey) while the turtles from Moreton Bay and Hervey Bay had similar numbers of prey (3.8 prey speeies per sample) (1 way ANOVA: $F_{2,38} = 9.57$; $p<0.001$). The comparison excluded Sandy Straits beeause of the small sample size and the Gold Coast - Jumpinpin samples because it was impossible to count the masses of fish bone in the gut contents.

The size, sex and maturity of the sampled turtles are listed in Tables 2-5. There were 27 males and 21 females and two unsexed turtles in the study group. The prey ingested was unrelated to sex or size because there was no significant

TABLE 3. Relative abundance by number of individuals of prey items from *Caretta caretta* gut contents (G) of beach washed turtles or faecal samples (F) from captured wild turtles from Hervey Bay (n=5) and Sandy Straits (n=2) areas. All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. The sample from specimen T79317 was a faecal sample. The remainder were from gut contents. Species present at less than 5% of a gut content are not listed.

	Hervey Bay					Sandy Strait	
Tag number	Q18573	T57853	-	Q22481	Z322	T79317	T22833
Date	11.01.96	25.11.95	27.01.98	19.12.96	24.09.92	13.06.95	11.06.95
Sex	♂	♂	♂	♂	♀	♀	♀
Maturity	Immature	Immature	Immature	Immature	Immature	Immature	Adult
Carapace length (cm)	79.4	80.9	95.2	83.4	104.0	71.0	94.1
Latitude	25°11'S	25°09'S	25° 08'S	24°43'S	25°01'S	25°42'S	25°45'S
Longitude	152°37'E	152°37'E	152°35'E	153°12'E	153°21'E	15°55'E	152°57'E
Prey Items							
Mollusc, bivalve							
Anadara trapezium	6%						100%
Atrina pectinata			87%				
Patro australis		25%					
Pinctada fucata	y			8%			
Mollusc, gastropod							
Velacumantis australis						99%	
Crustacea, hermit crab							
Dardanus imbricatus				75%			
Crustacea, brachyuran crab							
Charybdis natator		25%					
Leucosia sp.			8%	8%			
Mutata sp.				8%			
Myra affinis					10%		
Portunus sanguinolentus		25%			90%		
Brachiopod							
Lingula murphiana	90%						
Fish , unidentified		25%					

difference in the number of prey species per gut sample between the sexes ($t=0.357$, $d.f.=47$, $p>0.05$) or by size of these large immature and adult-sized turtles (regression analysis: $F_{1,48}=0.005$, $p>0.25$; $r^2=0.0001$, $df=48$, $p>0.05$).

FEEDING OBSERVATIONS. *C. caretta* in eastern Australia used four modes of behaviour to locate and obtain their prey.

Mining. Some *C. caretta* in shallow soft-bottom habitats of Moreton Bay located buried infaunal prey items by 'mining' (Limpus et al., 1994; Preen, 1996). The turtles use sweeping motions of their front flippers to dig shallow meandering trenches ~1.5m wide with the advancing edge 0.3-0.45m deep. This mining action resembles the front flipper actions used during nesting behaviour when the ♀ is digging or filling in the body pit (Bustard et al., 1975). Thick and thin shelled bivalves and polychaetes (Preen, 1996) of exposed infauna are then crushed and ingested by the turtles. While this feeding behaviour has been regularly observed in sea grass meadows of Moreton Bay, we have not observed it with *C. caretta* in sandy lagoons of the southern Great Barrier Reef. To be effective, mining requires a substrate that will not readily collapse as trenches are dug. The seagrass root-mass provides this short term stability in Moreton Bay.

Biting into substrate surface. In the southern Great Barrier Reef, some *C. caretta* feed on molluscs living within the top few centimetres of sand of coral-reef lagoon habitat (Limpus, 1978; Moodie, 1979). 'The turtle walks across the bottom biting up mouthfuls of the molluscs and sand, blowing out the latter with water before

TABLE 4. Relative abundance by number of individuals of prey items from *Caretta caretta* gut contents of beach washed turtles or faecal samples from captured wild turtles from Moreton Bay (n=21). All samples were obtained from turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. y' denotes that the species was present in the gut sample at less than the 5% level. Samples from specimens K7489, T51210 and T53780 were faecal samples. The remainder were from gut contents. Not all species present in all samples are listed. * Where there was a very large difference in the size of prey items the abundance has been adjusted to reflect the relative volume of the species.

Tag number	J49809	J51131	J51658	J53275 *	J53276	K7489	Q10419
Date	12.09.89	4.09.90	18.01.91	22.06.91	24.06.91	29.05.97	29.09.91
Sex	♂	♀	♀	♂	♂	♀	♀
Maturity	Immature	Immature	Immature	Immature	Immature	Adult	Immature
Carapace length (cm)	90.9	62.5	77.1	97.7	86.2	91.5	74.6
Latitude	-	27°11'S	27°18'S	27°22'S	27°12'S	27°18'S	27°31'S
Longitude	-	153°2'E	153°04'E	153°23'E	153°22'E	153°22'E	153°23'E
Prey Items							
Mollusc, gastropod							
Monilea callifera							
Pyrazus ebeninus							
Strombus campbelli							
Mollusc, bivalve							
Anadara trapezium							
Antigona lamellaris							
Atrina pectinata							
Cardita incrassata							
Eucrassatella cumingii							
Solen vaginoides							
Trichomya hirsuta							
Crustacea, hermit crab							
Dardanus imbricatus							
Crustacea, brachyuran crab							
Eucrate dorsalis	12%	50%	100%	30%	16%		100%
Galene bispinosa				10%	12%		
Leucosia sp.	12%						
Portunus pelagicus	38%					100%	
Portunus sanguinolentus	38%	50%		20%	6%		
Thalamita sima					y		
Portunid Crab, unidentified 1					42%		
Portunid Crab, unidentified 4					18%		
Crab, unidentified 9							
Crustacea, *Squilla* sp.					y		
Echinoderm, sea urchin							
Echinoderm, bêche-de-mer							
Cnidarian, sea whip				20%			
Porifera, sponge				20%			
Urochordate, ascidian							
Fish, porcupine fish							
Fish, unidentified							

TABLE 4. (*cont.*).

Tag number	Q10460	T51210	T53780	T70057	T83099	X10789*	X10791
Date	23.05.92	10.11.90	30.08.90	19.09.95	30.05.95	7.10.96	17.05.96
Sex	-	♂	♀	♂	♀	♂	♂
Maturity	-	Immature	Immature	Immature	Immature	Adult	Immature
Carapace length (cm)	-	81.4	92.5	86.0	78.9	105.8	78
Latitude	27°08'S	27°21'S	27°26'S	27°15'S	27°21'S	27°25'S	27°21'S
Longitude	153°22'E	153°24'E	153°21'E	153°04'E	153°07'E	153°31'E	153°04'E
Prey Items							
Mollusc, gastropod							
Monilea callifera						90%	
Pyrazus ebeninus						5%	
Strombus campbelli							
Mollusc, bivalve							
Anadara trapezium			100%				
Antigona lamellaris							
Atrina pectinata							
Cardita incrassata							
Eucrassatella cumingii							
Solen vaginoides		99%					
Trichomya hirsuta							
Crustacea, hermit crab							
Dardanus imbricatus							
Crustacea, brachyuran crab							
Eucrate dorsalis				33%	57%		25%
Galene bispinosa				14%	29%		55%
Leucosia sp.							
Portunus pelagicus							10%
Portunus sanguinolentus					10%	y	
Thalamita sima		y		48%			
Portunid Crab, unidentified 1	50%				y		
Portunid Crab, unidentified 4							
Crab, unidentified 9							5%
Crustacea, *Squilla* sp.				y			
Echinoderm, sea urchin							
Echinoderm, bêche-de-mer						5%	
Cnidarian, sea whip							
Porifera, sponge							
Urochordate, ascidian							
Fish, porcupine fish							
Fish, unidentified	50%				y		

crushing and swallowing the shells' (Limpus, 1978).

Picking off the substrate surface. C. caretta will feed on visible prey items on the substrate surface. Limpus (1973) described *C. caretta* grasping, crushing and tearing a 19cm long clam, *Tridacna maxima*, from the substrate surface of a coral reef. An adult male loggerhead (CCL= 94.2cm) was observed pulling a large distended anemone (*Stichodactyla haddoni*) from the surface of the sandy substrate on the Moreton Banks of Moreton Bay (Limpus et al., 1994). Several large immature *C. caretta* which were not engaged in 'mining' at the time have been captured while feeding on portunid crabs, *P. pelagicus*, on the bottom over the Moreton Banks (Limpus et al.

TABLE 4. (*cont.*).

Tag number	Z107	Z1806	Z1819 *	Z3014*	Z3057		-
Date	18.04.93	28.06.96	20.07.96	12.03.98	22.01.98	2.01.92	29.01.91
Sex	♂	♀	♂	♂	♂	♂	-
Maturity	Adult	Immature	Adult	Immature	Immature	Immature	Adult?
Carapace length (cm)	95.5	78.4	96	91.0	-	86.3	93.7
Latitude	26°57'S	26°57'S	27°11'S	27°14'S	27°26'S	27°23'S	27°12'S
Longitude	153°09'E	153°09'E	153° 22'E	153°11'E	153°11'E	153°12'E	153°07'E
Prey Items							
Mollusc, gastropod							
Monilea callifera							
Pyrazus ebeninus							
Strombus campbelli					91%		
Mollusc, bivalve							
Anadara trapezium						61%	
Antigona lamellaris				75%	5%	y	
Atrina pectinata	33%					y	
Cardita incrassata						11%	
Eucrassatella cumingii	17%						
Solen vaginoides							
Trichomya hirsuta		100%		12%			
Crustacea, hermit crab							
Dardanus imbricatus	17%						
Crustacea, brachyuran crab							
Eucrate dorsalis			35%		y		55%
Galene bispinosa			35%		y		15%
Leucosia sp.	17%						
Portunus pelagicus						y	
Portunus sanguinolentus	17%		y		y	y	15%
Thalamita sima							
Portunid Crab, unidentified 1							
Portunid Crab, unidentified 4							
Crab, unidentified 9							
Crustacea, *Squilla* sp.			10%				
Echinoderm, sea urchin				9%	y		
Echinoderm, bêche-de-mer							
Cnidenan, sea whip							
Porifera, sponge							7%
Urochordate, ascidian						14%	7%
Fish, porcupine fish			15%				
Fish, unidentified			y				

1994; CJL, DJL, MAR unpubl. obs.). Individual turtles may be persistent in their attempts to obtain an individual food item. For example, an adult *C. caretta* was observed for ~15 minutes as it attempted to bite a large *Trochus* sp. from a crevice in a coral boulder on Wistari Reef in the southern Great Barrier Reef. The crevice was too narrow for the turtle's jaws to reach the mollusc. The turtle repeatedly circled and nudged the boulder apparently searching for an alternative access to the food and regularly returned to push into the crevice. *C. caretta* are occasionally captured by amateur anglers in Moreton Bay

TABLE 5. Relative abundance by number of individuals of prey items identified in the gut contents of beach washed *Caretta caretta* from the Gold Coast - Jumpinpin area (n=8). All samples were obtained from gut contents of turtles that had been feeding immediately prior to their death. Relative abundance values are summarised only for those species comprising >5% of the total sample for the turtle. y' denotes that the species was present in the gut sample at less than the 5% level. Not all species present in all gut contents are listed.

Tag number	-	UQ91/1533	Z3051	Z3052	Z3053	Z3054	Z3116	Z3117
Date	24.10.91	13.12.91	14.1.98	14.1.98	14.1.98	14.1.98	19.03.98	19.03.98
Sex	♂	♀	♂	♂	♂	♀	♂	♂
Maturity	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Adult
Carapace length (cm)	96	97	100.5	99.7	99.5	92.7	95.8	93.6
Latitude	28°02'S	27°54'S	27°52'S	27°55'S	27°53'S	27°55'S	27°42'S	27°43'S
Longitude	153°26'E	153°24'E	153°25'E	153°25'E	153°25'E	153°25'E	153°27'E	153°27'E
Prey Items								
Mollusc, gastropod								
Tonna tessellata		20%						
Crustacea, brachyuran crab								
Charybdis natator		20%	y		y			
Matuta sp.	20%							
Portunus sanguinolentus	20%		y		y			
Ranina ranina	40%	20%	y		y			
Fish, mixed species including flathead (*Platycephalus* sp.), whiting (*Sillago* sp.), flounder (*Pseudorhombu* sp.), wrasse (Labridae), bigeye (*Priacanthus* sp.)	20%	40%	>90%	>95%	>90%	>95%	>95%	>90%

when the turtles ingest hooks baited with fish that lie on the bottom.

Plucking from the water column. C. caretta will feed within the water column (Limpus, 1978; CJL, MAR unpubl. obs.). *C. caretta* living on the reef edge at Heron Island in the southern Great Barrier Reef grazed on clusters of goose-neck barnacles, *Lepas* sp., growing on floating timber. When swarms of the jellyfish, *Pelagia noctiluca*, drifted over the coral reefs near Heron Island, adult and large immature *C. caretta* of all sizes present cease feeding on their normal food of benthic molluscs (Moodie, 1979) and rise to feed at or near the surface on these jellyfish. In contrast, *C. caretta* in Moreton Bay has not been observed to feed on the abundant *Catostylus mosaicus* within their close proximity.

In the Queensland Shark Control Program, drumlines (large hooks suspended near the surface from a float) are baited with dead fish to catch sharks (Kidston et al., 1992). *C. caretta*, especially off Point Lookout (27°26'S, 153°32'E) and the Gold Coast, regularly eat the fish baits on drumlines and are hooked. Many of these turtles have been tagged on release. Tag recoveries indicate that *C. caretta* learn to seek food from such artificial sources and return regularly to the hooks. In an extreme case, an adult male *C. caretta* (tag T74407) was hooked at least 18 times on the baited drumlines off Point Lookout between 06 December 1993 and 09 September 1995. These turtles demonstrate that *C. caretta* will scavenge on food items floating at or near the water surface in addition to taking live food.

These four feeding modes appear to be employed by the turtles examined in the present study. The brachiopod, *L. murphiana* (Table 3), and the bivalve, *S. vaginoides* (Table 4), burrow deeply within the substrate and can occur in dense aggregations (de Villiers & Hodgson, 1993). These species can be obtained in quantity only by mining. The scallop, *A. balloti* (Table 2) and the many hermit crabs (Tables 2-4) which do not burrow would have been taken from the substrate surface. The species that burrow to only a limited extent (*A. trapezium*, *A. pectinata*, *S. campebelli*) would be obtained from beneath the surface by biting into the substrate. When a turtle scavenges discarded bycatch from trawlers (e.g. Table 5), it is simply feeding on prey items on the substrate surface or in the water column. Differences in prey encounter rate and processing may influence a turtle's choice in procuring food.

When burrowing bivalves and brachiopods were consumed in large numbers, presumably by mining, few gastropods or crabs were consumed. It would involve 'biting' as well as infaunal mining to obtain such variety. When crabs were consumed, very few, if any, bivalves were found in the gut contents. When bivalves did occur with crustaceans, it was usually superficially burrowing bivalves like the scallop *A. balloti* or razor clams *A. pectinata* that were also targeted.

Large fragments of prey exoskeleton can cause blockage of the intestine with resulting death of the turtle: T22833 (Table 3) was found floating and moribund with a necrotic large intestine blocked with a compacted mass of *A. trapezium*.

DISCUSSION

Extant turtles do not have teeth. Rather *C. caretta* has keratinised sheaths to its jaws that are specialised for grasping and fragmenting hard-bodied food items (Thompson, 1980). With marine turtles, the food is pushed from the mouth through the oesophagus to the stomach using water and a hyoid pump (Bjornadal, 1985; C. Limpus, unpubl. data). The oesophagus is lined with backwardly projecting keratinised spines that act as a filter system to allow the food to be pushed easily down the throat while impeding its return back from the stomach but not impeding the return flow of water (Thompson, 1980). The back flow of water is also used to flush sand and other small particles from the buccal cavity when the turtle bites up a mouthful of prey and sediment (Limpus, 1978). The thick, keratinised epidermal surfaces of the buccal cavity and throat provide protection to the turtles during ingestion of the sharp and abrasive surfaces of the exoskeletal fragments of molluscs and crustaceans. This thick epidermal lining to the mouth and throat also provides protection from envenomation during ingestion of venomous prey such as *Physalia* and jellyfish like *P. noctiluca*. Once the food bolus has passed beyond the oesophagus, acid secretions by the stomach would inhibit discharge of cnidarian stinging cells (Sutherland, 1983). During the pelagic life history phase, the young *C. caretta* feed in surface waters (Carr, 1986). Those in later life history phases that live in the shallower inshore waters, have changed their feeding behaviour to utilise prey items on the sea floor.

The *C. caretta* in this study area were carnivorous, consuming a wide variety of benthic organisms. Prey items ranged from a single to hundreds of animals per gut sample. Quantifying prey abundance was highly problematic as our methods give a minimum estimate of the number of each species per sample. Preen (1996) observed abundant broken mollusc shells in feeding scars left from infaunal mining, suggesting that much shell, including the identifying components, is not swallowed. Alternatively, identifiable features of prey items such as thin-toothed mollusc radula may accumulate in the gut, resulting in exaggerated numbers. For example, a count of the radulae of *S. campbelli* in sample T89145 indicated 541 individuals were consumed, yet only 21 spires were recorded from the shells retrieved. Scyphomedusae (jellyfish), hydromedusae, siphonophores and other soft-bodied macroplankton are significant prey of pelagic post-hatchling *C. Caretta* (Bleakney, 1967; van Nierop & den Hartog, 1984; Plotkin et al., 1993). These soft bodied prey without skeletons are rapidly digested (Plotkin et al., 1993; van Nierop & den Hartog, 1984) and therefore, it may be difficult to identify them in gut content studies. However, many of these turtles were freshly dead and such prey items would be recognised in the anterior of stomachs if fed upon immediately prior to death. This was not the case. While the present study underestimates the occurrence of soft bodied prey, it is concluded that *C. caretta* in their non-pelagic phase does not feed extensively on large, soft-bodied planktonic organisms. Even so, the ingestion of charcoal and tree bark in some turtles suggests at least some surface feeding. It appears that when large swarms of some species of jellyfish are available, large immature and adult *C. caretta* will temporarily abandon benthic foraging in favour of plucking these items from the water column, a reversion to the feeding behaviour used during the previous pelagic phase (Frick et al., 1999). Given the finite time for food passage through the gut, a gut content or single faecal sample provides only a 'snapshot' of the diet and probably retains fewer species than were actually consumed.

C. caretta in S Queensland have unpredictable and opportunistic diets that result from selective foraging modes and chance encounters with prey patches. Our study was based primarily on stranded *C. caretta* and so foraging areas could only be approximated to broad regions. Large immature and adult *C. caretta* are specialised for feeding on slow moving, hard bodied invertebrate prey (Conway, 1994; Dodd, 1988; Plotkin et al., 1993; Moodie, 1979). As a generalised carnivore, different prey species can be expected to dominate *C. caretta* diet in different regions.

Turtles from the same locality have a common set of potential prey species yet individuals do not necessarily consume the same prey. Moodie (1979), and Conway (1994) determined in studies of the loggerheads from the southern Great Barrier Reef and the Northern Territory, respectively, that prey availability at feeding sites was different to the relative frequency of those species in the turtle gut contents. The present study also shows that individuals may feed on a very limited range of species and use specialised methods such as infaunal mining to expose the prey. Thus some variability of the diet may be attributed to individual food preference. As in the Northern Territory and GBR (Conway, 1994; Moodie, 1979) we find no correlations in diet for sex, size, season, or year. Furthermore, Moodie (1979) found that turtles foraging over the same section of coral reef were each selecting a different species of mollusc. Yet the same turtles would rise to the surface to consume jellyfish that sporadically drifted over this reef in large numbers (CJL, pers. obs.). The extent to which *C. caretta* is obtaining nutritional components via a strategy of foraging on diverse taxa or is merely optimising available food sources that can be gathered with minimum energy expenditure is not addressed herein.Brachiopods are here identified for the first time in the diet of *C. caretta.*

Fish were present in samples other than those from the Gold Coast - Jumpinpin region. Frick (1997) suggested that fish are captured alive but it is more likely that they are scavenged, especially from discarded trawler bycatch (Shoop & Ruckdeschel, 1982; Plotkin et al., 1993).

With regular trawling, there is the potential for aggregating *C. caretta* that scavenge discarded bycatch in the trawled area and hence increasing their risk of capture and death. Once the turtle is associated with a chosen area such as an internesting refuge (Limpus & Reed, 1985) or feeding on a reliable food source (feeding off baited shark hooks, this study), they can be persistent with the association despite other disturbances or human-related perturbations.

C. caretta, through their diet, has additional unquantified interactions with a number of coastal fisheries. Commercially fished species such as the sand crabs *P. pelagicus* and *P. sanguinolentus*, the spanner crab *R. ranina* and the scallop *A. balloti*, are targeted as food by some *C. caretta.* Potentially more significant to fisheries is the role of *C. caretta* in the life cycle of the ascaridoid nematode *Sulcascaris sulcata*, a parasite of commercial scallops. *C. caretta* is the definitive host of *S. sulcata* (Sprent, 1977) with the adult worms inhabiting the stomach and intestine while eggs are shed to sea with faecal material. Molluscs are the secondary host to the larval worms and immature *S. sulcata* are frequently found in the adductor muscles of large bivalves, especially *A. balloti* (Cannon, 1978). The parasite completes its life cycle when the mollusc is eaten by *C. caretta.* This parasite can cause loss of fisheries production in areas where there is coincidence of large numbers of *C. caretta* and scallops (Lester, 1980). The occurrence of *C. caretta* off the Bundaberg coast where scallops are abundant enough to form a significant part of their diet, has the potential for maintaining locally elevated levels of infection of scallops by *S. sulcata.*

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